

A RAPID ASSESSMENT OF CORAL REEF COMMUNITY STRUCTURE AND DIVERSITY PATTERNS AT NAVAL STATION GUANTÁNAMO BAY, CUBA

*Mark Chiappone, Kathleen Sullivan-Sealey,
Georgina Bustamante and John Tschirky*

ABSTRACT

Ten shallow (<20 m) reefs at Naval Station Guantánamo Bay, southeastern Cuba, were surveyed during July–August 1996 to evaluate topographic complexity and community structure with respect to depth-related zonation and potential sedimentation impacts from the Guantánamo River. While the methods employed were not novel, coral reefs in the study area had not been previously studied and, because of low human population density, may provide useful comparisons to more disturbed reefs in the Caribbean. On leeward and windward sides of the Bay, four shallow (5 m) and four deeper (10 m) spur-and-groove reefs were surveyed, along with two reefs within the mouth of the Bay. On each reef, four 25-m transects were oriented perpendicular to shore on four haphazardly selected spurs and used to randomly select 1 m × 1 m quadrat locations. Benthic coverage using point-intercept counts and topographic complexity using the chain-length method were quantified within quadrats. All sampled reefs were dominated by algae, especially algal turfs, and stony corals. Mean percent algal cover among reefs ranged from 50 to 78%, while coral cover ranged from 11 to 49%. Analysis of variance showed that depth was more important than location in explaining the variability in mean coral cover. Cluster analysis using percent coverage of all bottom types and relative coral cover confirmed that reefs at the same depth were more similar in benthic composition. Several species considered to be less tolerant of sedimentation, however, were more abundant on windward reefs, suggesting that differences in sedimentation between windward and leeward areas may affect relative species abundance, but not total coral cover. Percent coral cover estimates from 9 of the surveyed reefs were well above recent values reported for other wider Caribbean reefs. The predominance of corals on these reefs is surprising, given the low abundance of herbivores (due to mass mortality and overfishing) and possible disease outbreaks affecting acroporid corals. These disturbances appear to have had less severe consequences than for other wider Caribbean reefs such as those in Jamaica and the Lesser Antilles, potentially due to the relative rarity of destructive storm events.

The island of Cuba is approximately 104,232 km² in area and has a coastline estimated at between 3500 and 5746 km by different authors (Wells, 1988). The insular shelf varies in width from 100 m off the coast south of Sierra Maestra to more than 140 km off Havana in the north. Maximum depths on the island shelf are approximately 100 m before abyssal depths are attained offshore at 1000 to 7000 m. Coral reefs occur throughout the insular shelf of Cuba, together with numerous islets and cays (Kuhlmann, 1974). The total reef extension for the island is estimated at 3966 km (Alcolado et al., 1997), partitioned into 2150 km on the north coast and 1816 km on the south coast (Wells, 1988). Several studies have described reef types and described species composition and community structure patterns, particularly on the northern and southwestern coasts (Kuhlmann, 1974; Zlatarski and Estalella, 1982; Herrera and Alcolado, 1986; Alcolado et al., 1993, 1997), but there is limited information for the southeastern coast.

The purpose of this study was to rapidly assess community structure and diversity patterns of previously undescribed coral reefs at the Naval Station Guantánamo Bay, south-eastern Cuba. The study was part of a broader rapid assessment program sponsored by the U.S. Department of Navy to provide a foundation for an integrated natural resources management plan (Sedaghatkish and Roca, 1999). The objectives of the coral reef assessment were three-fold: (1) to inventory the sessile benthic flora and fauna associated with reefs; (2) to describe depth-related zonation patterns; and (3) to evaluate the potential impact of Guantánamo River outflow on reefs located on the leeward side of the Naval Station. The study objectives were met by measuring topographic complexity, benthic coverage, and coral diversity patterns during 3 wks of sampling in July–August 1996. The study area's relatively remote location, low human population density, and similar zonation structure to that described for many Caribbean reefs may provide useful comparisons to more impacted coral reef environments.

STUDY AREA

The U.S. Naval Station at Guantánamo Bay is situated at the southeastern tip of Cuba at 19°15'N, 75°9'W (Fig. 1). Established in 1903, the Naval Base occupies roughly 117 km² (45 mi²) of Cuban territory and has 13.9 km of coastline. The total population of the Naval Station as of June 1996 was 4673 residents, represented by 1751 military personnel and 2942 civilians.

The Guantánamo Bay area climate is hot and dry, with minimum air temperatures of 18–19°C during January–February and maximum temperatures of 28–30°C during July–August. Precipitation ranges from 400–837 mm yr⁻¹, with monthly averages of 12–37 mm during the winter to 128 mm during the summer. The terrestrial area of the Naval Base is dominated by tropical dry forests, circumscribed by an array of coastal environments including mangroves, seagrass beds, rocky shores, and coral reefs (Sedaghatkish and Roca, 1999). Although high Pleistocene cliffs dominate the Caribbean coastal entrance to the bay and appear to have similar zonation patterns to Holocene reefs, these features have not been adequately studied. The shelf slope is roughly 35°, which contrasts significantly with a slight slope angle (>2°) on the western Cuban shelf. Although several rivers occur within and near the study area, the most notable being the Guantánamo River, overland runoff (10 mm) and subterranean runoff (5 mm) appear to be relatively insignificant. The Guantánamo Bay area, in fact, receives the lowest amount of river runoff on the island. Tides on the southern coast are semi-diurnal with a 0.5–1 m range in tidal height and currents are predominately from the east and northeast (Grant and Wyatt, 1980).

Distinct reef zones along a depth gradient on windward and leeward sides of the Naval Station were recognized during reconnaissance snorkel and SCUBA surveys: reef flat/breaker zone at 0.1- to 2-m depth; spur and groove at 5-m depth; spur and groove at 10-m depth; deep fore reef slope; and fore reef escarpment (Fig. 2). A second inshore-to-offshore zonation pattern was evident off Phillip's Park near the mouth of Bay: shallow spur and groove, sparse seagrass and sand, patch reefs, deeper seagrass, and deeper spur and groove. Shallow spur-and-groove reefs occur immediately offshore of sandy beaches, or steep, vertical rocky shores. On the windward and leeward sides of the Bay, coralline spurs are oriented in a north-to-south direction, indicative of the direction of predominant swell. Within the mouth of the bay, spurs are oriented east-to-west. Shallow spurs near the mouth of the bay are of much lower profile (generally <3 m vertical relief), upwards of 30 m in length, and up to 3 m wide. On windward and leeward coasts, spurs occur offshore of a breaker zone with localized dominance by *Acropora palmata*, *Millepora complanata*, and octocorals such as *Gorgonia ventalina* (Fig. 2, top). The predominant benthos are mostly turf algae and octocorals overlying an *A. palmata* framework. Seaward of the breaker zone is the shallow spur-and-groove system (Fig. 2, middle). Spurs are approximately 25 m in length or shorter, roughly 2–3 m wide, and as shallow as 3 m in some places. Closer to shore, individual spurs often merge. Grooves

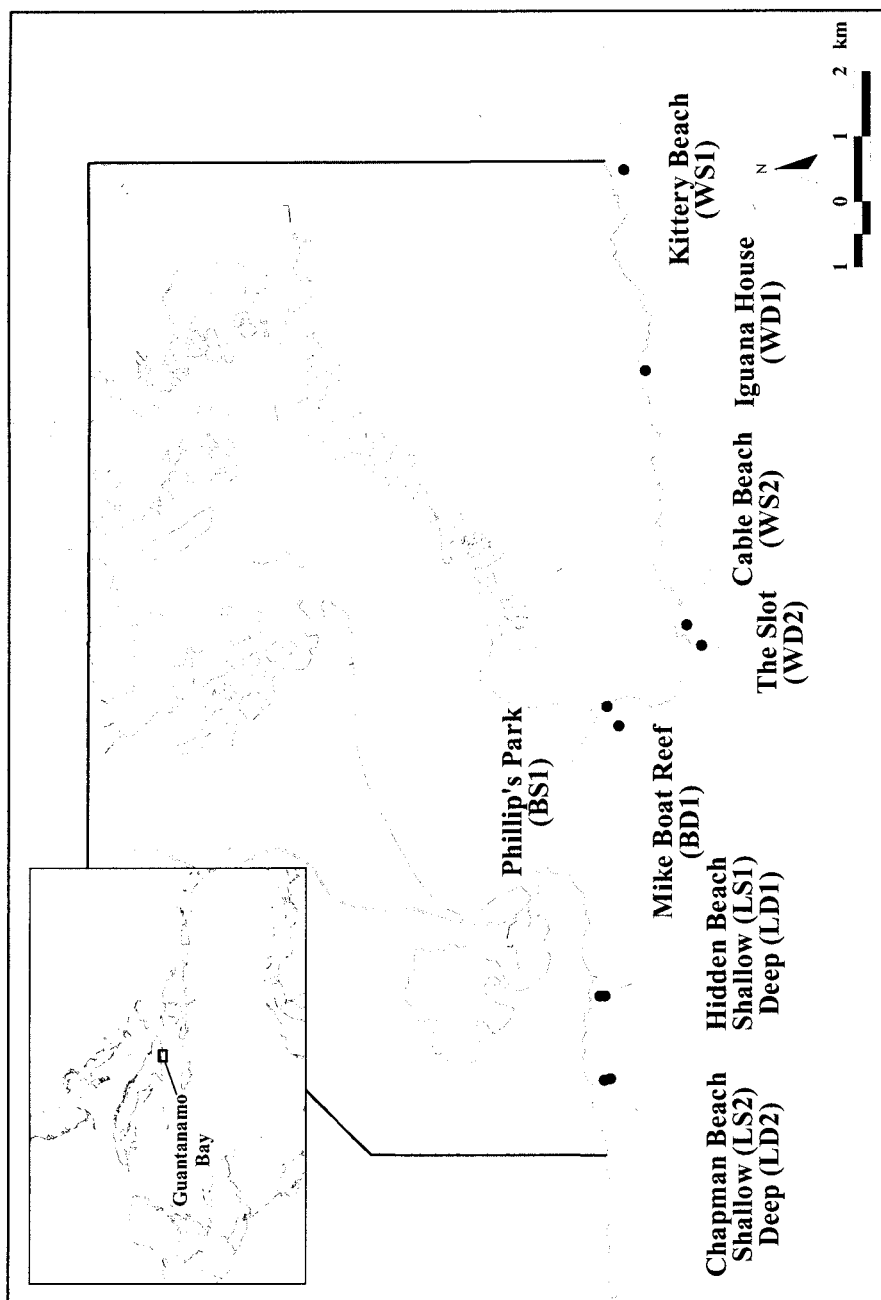


Figure 1. Spur-and-groove reefs sampled at Guantánamo Bay, southeastern Cuba.

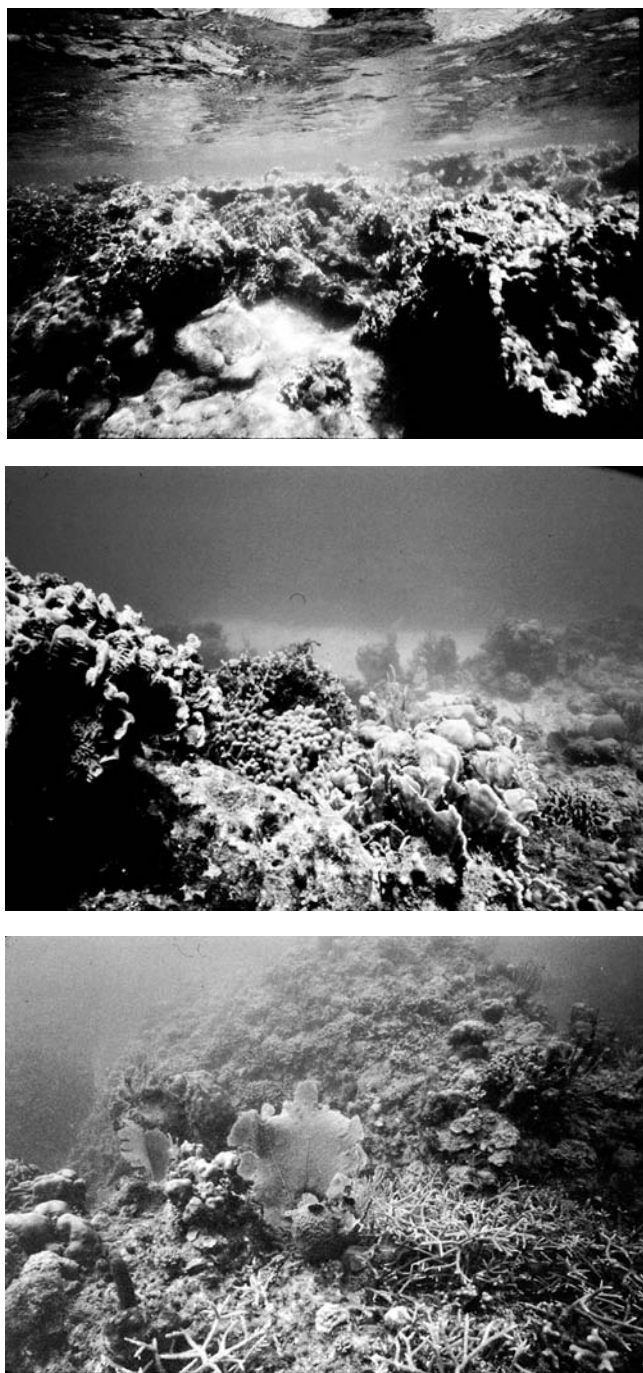


Figure 2. Reef zonation patterns at Guantánamo Bay Naval Station, southeastern Cuba. Reef flat and breaker zone showing *Acropora palmata* substratum at 0.5–1 m depth (top). Shallower spur-and-groove zone at 5-m depth (middle). Deeper spur and groove zone at 10-m depth, showing a predominance of large *Montastraea* spp. colonies and living and dead *A. cervicornis*, similar to historical mixed zone described for Jamaica.

Table 1. Depth range of transects, mean (1 SD) depth of surveyed quadrats, and mean (1 SD) topographic complexity (TC) for reefs surveyed in Guantánamo Bay Naval Base, Cuba. Sample size was 40 1-m² quadrats for each reef.

Reef type/local name (code)	Depth (m)	Quadrat depth (m)	TC (cm/m)
Windward, shallow reefs			
Kittery Beach (WS1)	4.8–8.1	6.42 (0.67)	156 (33)
Cable Beach (WS2)	3.9–9.6	6.80 (1.21)	148 (38)
Windward, deeper reefs			
Iguana House (WD1)	8.1–12.0	9.97 (0.92)	159 (33)
The Slot (WD2)	10.2–13.5	11.48 (0.91)	180 (44)
Leeward, shallow reefs			
Hidden Beach Shallow (LS1)	3.6–7.2	6.09 (0.67)	148 (27)
Chapman Beach Shallow (LS2)	3.3–7.2	5.29 (0.78)	147 (31)
Leeward, deeper reefs			
Hidden Beach Deep (LD1)	7.5–11.7	8.82 (0.92)	179 (44)
Chapman Beach Deep (LD2)	6.3–12.3	9.62 (1.56)	140 (23)
Bay, shallow reefs			
Phillip's Park (BS1)	3.0–5.4	3.93 (0.70)	121 (13)
Bay, deeper reefs			
Mike Boat Reef (BD1)	8.1–12.6	9.31 (1.14)	162 (27)

consist mostly of coarse, calcareous sediments comprised of *Halimeda* sand. Measurements of 15 individual spurs at four reefs showed that the change in slope with distance from shore averages 0.06 (range = 0.01–0.16), i.e., an increase of 1.5-m depth per 25-m distance. The seaward edge of the spurs terminates at 8-m depth in an area with a mixture of sand and/or sparse seagrass (*Syringodium filiforme*).

Seaward of the shallow spur-and-groove system is the mid-depth (10 m) spur-and-groove system (Fig. 2, bottom). Spurs are relatively wide (3–5 m), range in depth from 7–8 m toward shore to 13 m at the seaward base, and have upwards of 4.5 m of vertical relief. This zone appears to be similar to the mixed zone, and to a lesser extent the *cervicornis* zone, described for other western Caribbean reefs such as the Cayman Islands and Jamaica (Goreau, 1959; Fenner, 1993). Measurements of 15 spurs at 4 reefs showed that the change in slope from a shoreward-to-seaward direction averages 0.07 (range = 0.01–0.14), i.e., an increase of 1.75 m per 25 m distance.

Offshore of the spur-and-groove system at 10-m depth is the deeper fore reef slope, which extends from 15- to 25-m depth. Deeper spurs end at about 15-m depth, and below this depth, the grooves become wider, while the spurs are narrower, of less relief, and have lower coral cover. The deeper reef slope terminates at roughly 25–27 m in a fore reef escarpment, or drop-off zone.

MATERIALS AND METHODS

Ten spur-and-groove reefs within the Naval Station Guantánamo Bay were surveyed for species richness and benthic community structure during July–August 1996 (Table 1). Benthic surveys were generally confined to less than 14-m depth and, except for two sites, all other reefs were accessed from shore. Two replicate reef areas were surveyed in each location (windward, leeward) and depth category (5 m, 10 m), except for only one shallow (BS1) and deep spur and groove reef (BD1) within the mouth of Guantánamo Bay (Fig. 1). Mean depth of quadrats surveyed for the five shallow spur-and-groove reefs ranged from 3.9 to 6.4 m, while mean sample depth for the five deeper spur-and-groove reefs ranged from 8.8 to 11.5 m.

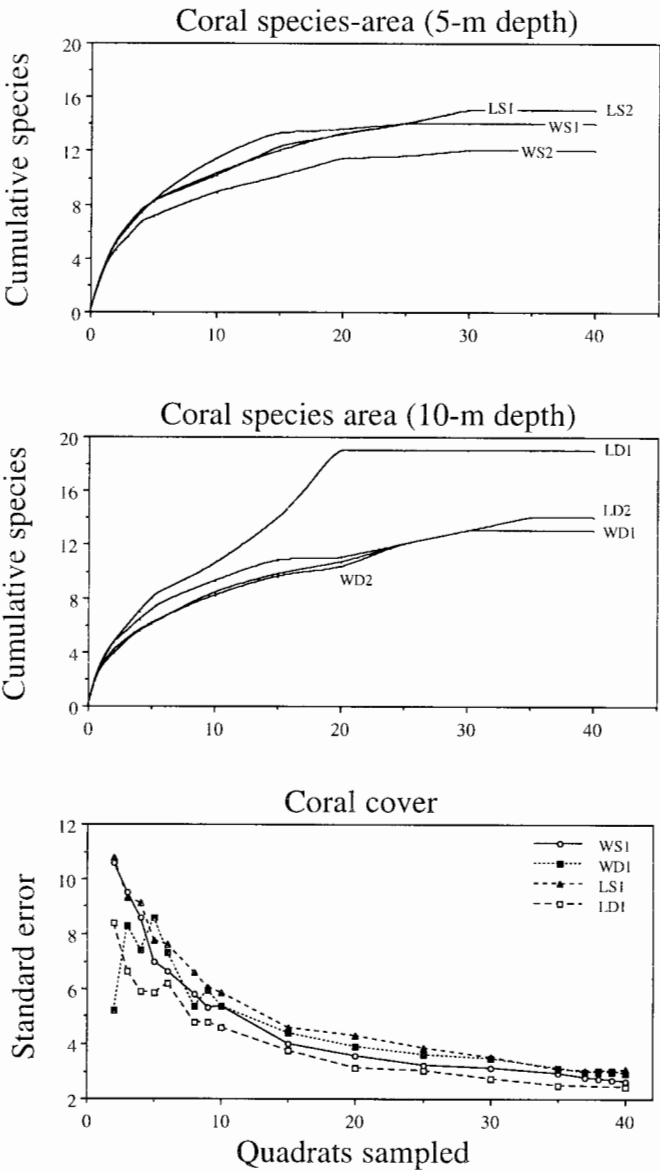


Figure 3. Cumulative number of coral species vs quadrats sampled for reefs at 5-m depth (top) and 10-m depth (middle) and standard error of percent coral cover vs number of quadrats sampled (bottom).

Randomly placed quadrats along line transects were used to estimate topographic complexity and coverage. In each general reef area, four coralline spurs were selected haphazardly and used to locate 25 m transects placed inshore to offshore (total of 10 reefs and 40 spurs). Quadrats measuring 1 m × 1 m were placed randomly along transects on each reef. The length of transect was chosen based on the length of spurs and the width of the desire depth interval based on apparent zonation patterns. Ten 1-m² quadrats were randomly placed along each of the four transects. The size of quadrats was selected based on the maximum size of organisms (i.e., generally no larger than 1 m in

diameter) in the study area. Topographic complexity, an integrated but indirect measure of disturbance, was measured using the chain-link method (Rogers et al., 1983; Aronson and Precht, 1995). A 2-m length of brass chain, marked in 10 cm increments, was placed across each 1 m × 1 m quadrat along the contours of the substratum and used to measure the length of chain versus a known linear distance. Ten measurements per spur for a total of 40 measurements per reef were obtained in this manner. Benthic coverage was estimated using point-intercept counts within quadrats (Ohlhorst et al., 1988). A 1-m² quadrat was divided by string so that 25 intersection points were contained within the area of the quadrat. For each reef, 1000 points were surveyed for bottom cover. The bottom type under each point was identified to the lowest taxonomic level possible.

Appropriate sample sizes were considered for the variables measured in this study using two techniques. Species-area curves (Gleason, 1922) for reef corals were used to evaluate the function of the cumulative number of species vs. quadrats sampled (Fig. 3). Our sample size of 40 1-m² quadrats was often twice the level of sampling needed to reach the asymptote in the curve. Sample size was also evaluated by comparing standard errors of particular parameters to sample-size functions (Fig. 3). This approach used a method described by Bros and Colwell (1987), in which the resolving power of various sample sizes is compared by examining the standard error of the mean vs. the number of samples. This relationship is theoretically a decreasing asymptotic function approaching zero, and the location of the region of greatest change in slope is a result of the relationship between the sample variance and the true variance. For our study, percent coral cover was selected as the metric to evaluate minimum sample size, based on the assumption that this variable would be the most indicative of patterns in community structure patterns related to depth and location. A bootstrapping technique was used to randomly select at least four draws per sample size over a range of sample sizes from 2 to $n - 1$. The region of greatest change in the four plots was approximately ten quadrats for coral cover (Fig. 2).

The parameters measured were used to test the null hypotheses of no differences among reefs in topographic complexity and benthic cover with respect to depth and location within the Guantánamo Bay Naval Station. Data collection was structured so that a two-way nested analysis of variance could be used, in which there were two levels or categories of depth (shallow vs. deep) and two levels of location (windward vs. leeward). In each depth-location combination, there were two reef sites comprising the nested term (random effect). The method of Sokal and Rohlf (1981) was used to determine how much of the total variability was due to location, depth, the interaction term, and the nested term in each of the models. The two reefs within the mouth of Guantánamo Bay (Phillip's Pier area) were not used in the model, because only one shallow and deep reef were surveyed in this area. The 40 1-m² quadrats per reef constituted the replicates used in the models. Data were tested for normality and variance homogeneity using the Kolmogorov-Smirnov Test for both discrete and continuous distributions, as well as Bartlett's Chi-square test, respectively (Zar, 1996). Although analysis of variance is robust to many types of non-normality (Underwood, 1981), it was determined that percent sponge cover and octocoral cover data could not be analyzed in this manner. Frequency distributions for these two variables were negatively skewed due to the large number of zero values in the data. It was determined that monotonic transformations for the other variables were necessary to remove the relationship between the variance and the mean. For mean percent algal and coral cover, an arcsine transformation was used ($\sin^{-1} \sqrt{p}$, where p is the decimal equivalent of the percentage), while a logarithmic transformation ($\log_{10} x$) was used for topographic complexity.

Relationships among depth, topographic complexity and benthic community structure were explored using correlation analysis (Zar, 1996). Due to the skewed distributions of sponge and octocoral coverage data, Spearman rank correlation coefficients were used. A sequential Bonferroni test was used to assess the table-wide significance of correlations, in order to control the probability of incorrectly rejecting one or more null hypothesis and to maintain the power of the statistical tests for detecting false null hypotheses.

Multivariate statistical techniques were used to evaluate patterns in species composition and relative abundance among reefs. Data from point-intercept counts for all bottom types were used to

compute similarity among reefs using the Percent Similarity Index, computed as $\text{Similarity } S = 200 * \{S \text{ minimum } (Y_{ij}, Y_{ik}) / (S(Y_{ij} + Y_{ik}))\}$, where Y_{ij} = score (i.e., percent cover) for the i^{th} species in the j^{th} sample and Y_{ik} = score for the i^{th} species in the k^{th} sample (Pielou, 1984). The index was summed for all species and functional groups identified in the samples. Pair-wise comparisons were made among reefs to construct a dendrogram from cluster analysis using a group-average sorting strategy (Pielou, 1984). Although the group-average sorting strategy has several disadvantages (i.e., hierarchy is irreversible, only inter-group value is shown), this method is generally preferable to other strategies (Field et al., 1982). These same procedures were also used to evaluate patterns in relative coral cover by species.

Diversity patterns of corals by depth and location were explored using data from point-intercept counts. The number of points represented by each species was used to compute diversity indices using the Shannon-Weaver Index, a measure that takes into account both species richness and evenness (Pielou, 1977). Diversity was calculated as $H'_c = S p_i \log p_i$, where H'_c = diversity based on cover, p_i = the proportion of points covered by the i^{th} species, and S indicates the summation over all i species. Natural logarithms (\log_e) were used to compute the indices. Evenness was computed as $J'_c = H'_c / H'_{\text{max}}$, where H'_c is as above and H'_{max} = logarithm of the number of coral species recorded.

RESULTS

Seventy-two benthic cnidarians distributed among two taxonomic classes were identified during the reef assessments (Table 2). Species were distributed among seven orders and 40 genera and 13 subspecies or forms were found. Twenty-nine species of octocorals among 12 genera were recorded. Identifications for 11 of the 29 species were confirmed by spicule preparations. Thirty-four species and ten forms or subspecies of stony corals were identified.

Ten spur-and-groove reefs were sampled for topographic complexity and benthic cover among three locations (windward, leeward, bay) and two depths (roughly 5 and 10 m; Table 1). Among the eight reefs in the ANOVA model, mean topographic complexity did not differ significantly with respect to location ($P > 0.50$, F-test) or depth ($P > 0.20$, F-test; Table 2). The two main factors combined accounted for only 7% of the variability in the data. Although not included in the model, reef site BD1 exhibited comparable topographic complexity to deeper spur-and-groove reefs on leeward and windward coasts, while reef site BS1 had considerably lower relief (<140 cm/m) than other shallow reefs.

Mean percent algal cover among reefs ranged from 50 to 78% (Fig. 4). Turf algae, crustose coralline algae, *Dictyota* spp., and *Halimeda* spp. comprised more than 90% of the total algal cover (Appendix). The dominant functional group was algal turf, whose mean percent cover among reefs ranged from 27–63%. Turf algae accounted for 51 to 83% of the total algal cover. Analysis of variance indicated no significant differences ($P > 0.05$, F-test) in total algal cover with respect to location or depth (Table 3). Mean coverage by *Dictyota* spp. at 5 m depth was greater on leeward reefs (11.8–16.3%) than windward reefs (4.3–5.1%). On windward reefs, coverage by *Dictyota* spp. was greater at 10 m depth, but on leeward reefs, coverage was greater at 5 m depth. Coverage by *Halimeda* spp. exhibited a similar pattern.

Mean percent coral cover ranged from 11 to 49% among the 10 reefs (Fig. 4). The lowest coverage was recorded at reef site BS1. Coral cover was consistently greater at 10-m depth (34.4–49.2%) than at 5-m depth (10.7–30.1%). Analysis of variance indicated significant differences in total coral cover with respect to depth ($P < 0.02$, F-test), but not location (Table 3). Depth accounted for 10% of the variability in the data. *Acropora*

Table 2. Systematic list of benthic cnidarians (Phylum Cnidaria) observed on reefs of Guantánamo Bay Naval Base, Cuba. Identification of octocorals marked with an asterisk (*) were confirmed using spicule preparations.

Class Hydrozoa
Order Athecatae
Family Stylasteridae
<i>Stylaster roseus</i> (Pallas)
Family Milleporidae
<i>Millepora alcicornis</i> Linnaeus
<i>M. complanata</i> Lamarck
Class Anthozoa
Subclass Ceriantipatharia
Order Antipatharia
Family Antipathidae
<i>Stichopathes lutkeni</i> Brook
Subclass Alcyonaria
Order Alcyonacea
Suborder Scleraxonia
Family Briareidae
<i>Briareum asbestinum</i> (Pallas)
Suborder Holaxonia
Family Anthothelidae
<i>Erythropodium caribaeorum</i> (Duchassaing and Michelotti)
Family Plexauridae
<i>Iciliogorgia schrammi</i> Duchassaing
<i>Eunicea calyculata</i> (Ellis and Solander)
<i>E. fusca</i> * Duchassaing and Michelotti
<i>E. laciniata</i> * Duchassaing and Michelotti
<i>E. mammosa</i> Lamouroux
<i>E. palmeri</i> Bayer
<i>E. succinea forma plantaginea</i> * Lamarck
<i>E. tourneforti forma tourneforti</i> Milne Edwards and Haime
<i>E. tourneforti forma atra</i> * Verrill
<i>Muricea atlantica</i> (Riess)
<i>M. muricata</i> (Pallas)
<i>Muriceopsis flavida</i> * (Lamarck)
<i>M. petila</i> * sp. nov.
<i>Plexaura flexuosa</i> * Lamouroux
<i>P. homomalla</i> (Esper)
<i>P. nina</i> * Bayer and Deichmann
<i>Plexaurella dichotoma</i> * (Esper)
<i>P. grisea</i> * (Kunze)
<i>P. nutans</i> (Duchassaing and Michelotti)
<i>Pseudoplexaura porosa</i> (Houttuyn)
Family Gorgoniidae
<i>Gorgonia flabellum</i> Linnaeus
<i>G. ventalina</i> Linnaeus
<i>Pseudopterogorgia acerosa</i> * (Pallas)
<i>P. americana</i> (Gmelin)

Table 2. Continued.

	<i>P. bipinnata</i> (Verrill)
	<i>P. rigida</i> (Bielschowsky)
	<i>Pterogorgia citrina</i> (Esper)
	<i>P. guadalupensis</i> Duchassaing and Michelin
Subclass Zoantharia	
Order Actiniaria	
Family Actiniidae	
	<i>Condylactis gigantea</i> (Weinland)
Family Aiptasidae	
	<i>Bartholomea annulata</i> (Lesueur)
Order Zoanthidea	
Family Zoanthidae	
	<i>Palythoa mammosa</i> (Ellis and Solander)
	<i>Zoanthus pulchellus</i> Duchassaing and Michelotti
Order Corallimorpharia	
Family Actinodiscidae	
	<i>Ricordea florida</i> Duchassaing and Michelotti
Order Scleractinia	
Suborder Astrocoeniina	
Family Astrocoeniidae	
	<i>Stephanocoenia michelinii</i> Milne Edwards and Haime
Family Pocilloporidae	
	<i>Madracis formosa</i> Wells
	<i>M. mirabilis sensu</i> Wells
Family Acroporidae	
	<i>Acropora cervicornis</i> (Lamarck)
	<i>A. palmata</i> (Lamarck)
Suborder Fungiina	
Family Agariciidae	
	<i>Agaricia agaricites forma agaricites</i> (Linnaeus)
	<i>A. agaricites forma carinata</i> Wells
	<i>A. agaricites forma danai</i> Milne Edwards and Haime
	<i>A. agaricites forma purpurea</i> (Lesueur)
	<i>A. lamarcki</i> Milne Edwards and Haime
	<i>A. tenuifolia</i> Dana
	<i>Leptoseris cucullata</i> (Ellis and Solander)
Family Siderastreidae	
	<i>Siderastrea radians</i> (Pallas)
	<i>S. siderea</i> (Ellis and Solander)
Family Poritidae	
	<i>Porites astreoides</i> Lamarck
	<i>P. porites forma porites</i> (Pallas)
	<i>P. porites forma furcata</i> Lamarck
	<i>P. porites forma divaricata</i> Lesueur
Suborder Faviina	
Family Faviidae	
	<i>Colpophyllia natans</i> (Houttuyn)
	<i>Diploria clivosa</i> (Ellis and Solander)

Table 2. Continued.

<i>D. labyrinthiformis</i> (Linnaeus)
<i>D. strigosa</i> (Dana)
<i>Favia fragum</i> (Esper)
<i>Manicina areolata mayori</i> Wells
<i>Montastraea annularis</i> (Ellis and Solander)
<i>M. cavernosa</i> Linnaeus
Family Meandrinidae
<i>Dendrogyra cylindrus</i> Ehrenberg
<i>Dichocoenia stellaris</i> Milne Edwards and Haime
<i>D. stokesi</i> Milne Edwards and Haime
<i>Meandrina meandrites meandrites</i> (Linnaeus)
<i>M. meandrites memorialis</i> (Wells)
Family Mussidae
<i>Isophyllastrea rigida</i> (Dana)
<i>Mussa angulosa</i> (Pallas)
<i>Mycetophyllia aliciae</i> Wells
<i>M. danaana</i> Milne Edwards and Haime
<i>M. ferox</i> Wells
<i>M. lamarckiana</i> Milne Edwards and Haime
<i>Scolymia cubensis</i> Milne Edwards and Haime
<i>S. lacera</i> (Pallas)
Suborder Caryophylliina
Family Caryophylliidae
<i>Eusmilia fastigiata</i> (Pallas)

cervicornis, *Agaricia tenuifolia*, *M. complanata*, *M. annularis*, *Porites astreoides*, and *P. porites* comprised the majority of coral cover throughout the study area (Appendix). Several species exhibited depth-related changes in coverage (Table 4). Coverage by *A. agaricites*, *Madracis mirabilis*, *M. annularis*, and *P. porites* was greater at 10-m depth, while coverage by *A. tenuifolia*, *M. complanata*, and *P. astreoides* was greater at 5-m depth. Some species exhibited patterns in coverage related to location. At 5-m depth, *A. agaricites*, *Diploria clivosa*, and *Siderastrea siderea* were more abundant on leeward reefs, while *M. annularis* was more abundant on windward reefs. At 10-m depth, *P. astreoides* and *S. siderea* were more abundant on leeward reefs.

Coral diversity and evenness metrics based on point-intercept counts mostly exhibited differences related to depth, but not location (Table 5). Coral diversity and evenness were consistently greater on shallower reefs; this pattern reflected the greater dominance by fewer species, most notably *M. annularis* and *P. porites*, at 10-m depth.

Mean percent sponge cover ranged from <1 to 8% (Fig. 4). Coverage was generally greater at 5-m depth (range of 1.2–7.9%) than 10-m depth (0.3–1.3%), and was inversely correlated ($P < 0.05$, Spearman rank correlation) with depth and coral cover. This result partly reflected the pattern of greater coverage by *Cliona langae* in shallower reefs (Appendix).

Mean percent octocoral cover ranged from 0.1 to 2.1% (Fig. 4). Octocoral cover was generally greater at 5-m (range of 0.7–2.1%) than 10-m depth (0.1–1.3%). While 16 spe-

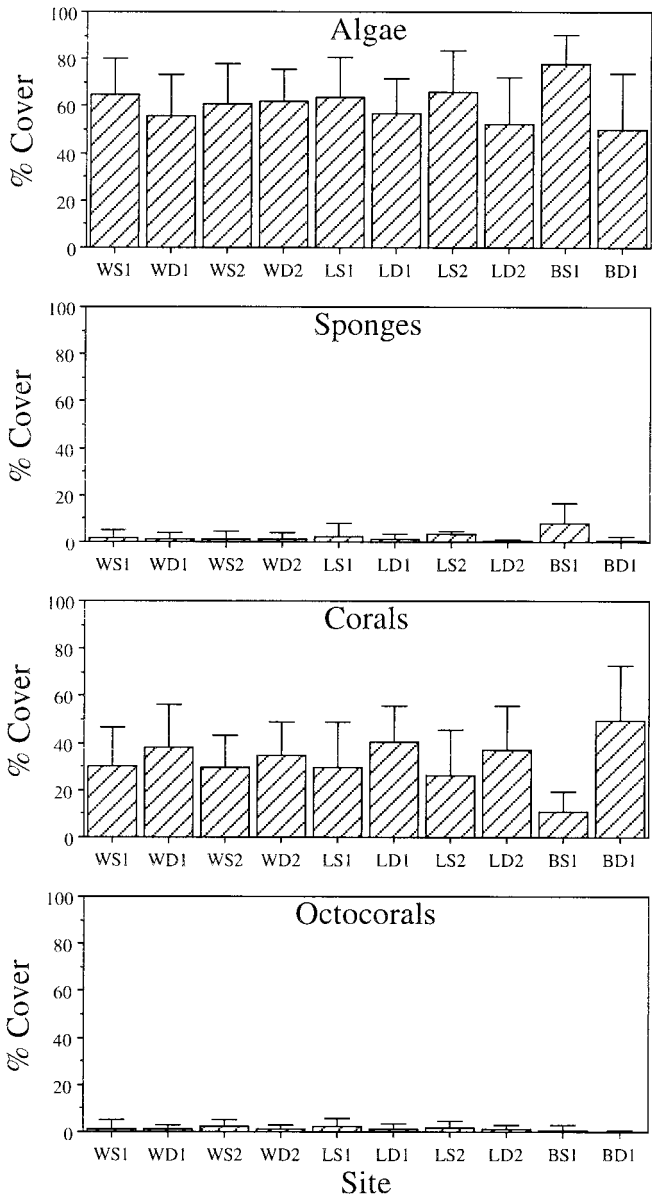


Figure 4. Mean percent cover of algae, sponges, stony corals, and octocorals in spur-and-groove reefs of Guantánamo Bay Naval Station, Cuba. Error bars represent one standard deviation. Sample size = 40 1-m² quadrats.

cies were recorded within quadrats among the 10 reefs (Appendix), no species on average comprised more than 0.9% of the sampled reef surface.

The similarity of sampled reefs was evaluated based on community composition (all bottom types) and relative coral cover. For all benthic types considered, the major pattern evident in the cluster analysis was the partitioning of reefs based on depth more than location (Fig. 5, left). The two reefs near the mouth of the bay (BS1, BD1) were the least

Table 3. Effects of location and depth on variation in mean topographic complexity, percent algal cover and percent coral cover on reefs of Guantánamo Bay Naval Base, Cuba. Data used were $\log_{10} (x+1)$ transformed topographic complexity and arcsine transformed ($\sin^{-1} \sqrt{x}$) coverage values. NS = $P > 0.05$, * = $P < 0.02$, ** = $P < 0.001$.

Variable	Factor	F-value	df	Significance	% variability
Topographic complexity	Depth	1.844	1	NS	6.37
	Location	0.379	1	NS	1.03
	Depth * Location	0.099	1	NS	6.54
	Site (depth * location)	7.860	4	**	12.56
Percent algal cover	Depth	9.797	1	NS	6.49
	Location	0.298	1	NS	1.47
	Depth * Location	2.048	1	NS	1.76
	Site (depth * location)	1.503	4	NS	1.12
Percent coral cover	Depth	29.487	1	*	9.57
	Location	0.142	1	NS	0.96
	Depth * Location	1.842	1	NS	1.30
	Site (depth * location)	0.656	4	NS	0.75

similar to other reefs. Overall similarity among eight of the ten reefs was relatively high (>60%), reflecting the dominance by similar benthos such as turf algae, *Dictyota* spp., *Halimeda* spp., and crustose coralline algae. Similarity of reefs based on relative coral cover also reflected the greater importance of depth (Fig. 5, right). The two reefs within the mouth of the bay were the least similar, but for different reasons. Reef site BSI was least similar to other shallow spur-and-groove reefs because of lower coral cover, as well as the low relative abundance of *A. tenuifolia*, *M. complanata*, and *M. annularis*. Reef site BDI exhibited greater coral cover compared to other deeper spur-and-groove reefs, however, most of the coverage was represented by a single species (*P. porites*). This contrasted with other 10-m reefs, where coral cover was dominated by *P. porites*, but also *M. annularis*, *P. astreoides* and *A. cervicornis* (Table 4).

Table 4. Dominant faunal elements (> 10% relative faunal cover) on reefs of Guantánamo Bay Naval Base, Cuba. WS = windward reefs at 5 m depth, WD = windward reefs at 10 m, LS = leeward reefs at 5 m, LD = leeward reefs at 10 m, BS = bay reefs at 5 m, and BD = bay reefs at 10 m.

Species	WS	WD	LS	LD	BS	BD
Stony corals (Scleractinia and Milleporina)						
<i>Acropora cervicornis</i>		X	X			
<i>Agaricia tenuifolia</i>	X		X			
<i>Montastraea annularis</i>		X	X	X	X	
<i>Porites astreoides</i>		X		X		X
<i>P. porites</i>	X	X		X		X
<i>Siderastrea siderea</i>			X		X	
Sponges (Demospongeae)						
<i>Cliona langae</i>					X	

Table 5. Diversity, evenness, and coverage parameters for stony corals on reefs of Guantánamo Bay Naval Base, Cuba. Shannon-Weaver diversity $H'_c = p_i \log_e p_i$, Evenness $J'_c = H'_c / \log_e S$, and S = number of species sampled in quadrats.

Reef type/local name (code)		Diversity (H' _c)	Evenness (J' _c)	S	Mean % cover
Windward, shallow reefs					
	Kittery Beach (WS1)	1.911	0.724	14	30.1
	Cable Beach (WS2)	1.945	0.783	12	29.3
Windward, deeper reefs					
	Iguana House (WD1)	1.399	0.546	13	37.9
	The Slot (WD2)	1.620	0.614	14	34.4
Leeward, shallow reefs					
	Hidden Beach Shallow (LS1)	2.132	0.858	12	29.8
	Chapman Beach Shallow (LS2)	2.298	0.849	15	26.1
Leeward, deeper reefs					
	Hidden Beach Deep (LD1)	1.750	0.594	19	40.2
	Chapman Beach Deep (LD2)	1.540	0.583	14	37.2
Bay, shallow reefs					
	Phillip's Park (BS1)	1.885	0.759	12	10.7
Bay, deeper reefs					
	Mike Boat Reef (BD1)	0.834	0.336	12	49.2

DISCUSSION

The coral reefs of Naval Station Guantánamo Bay comprise a fringing reef system with well-developed spur-and-groove formations on the shallow and deeper fore reef slope from 4 to 20 m depth. Like elsewhere in Cuba, fringing reefs occur on the insular platform where the island shelf is relatively narrow (Kuhlmann, 1974; Zlatarski and Estalella, 1982). There were similar species richness and dominance patterns of corals on reefs of Guantánamo Bay Naval Station as on other Caribbean reefs, particularly in the western Caribbean such as those in Jamaica, Belize, and the Cayman Islands (Edmunds et al., 1990; Fenner, 1993). Previous studies of other Cuban reefs have shown that the dominant constructional elements in general are *A. palmata*, *A. cervicornis*, *D. strigosa*, *M. annularis*, *M. cavernosa*, *M. complanata*, *P. astreoides* and *S. siderea* (Kuhlmann, 1974). In addition to these species, *A. tenuifolia* was locally abundant at 5-m depth in the study area. This pattern is similar to other western Caribbean locations, such as Belize, where spurs at 3–6 m depth can be dominated by *A. tenuifolia* (Aronson and Precht, 1995).

While our surveys yielded 44 stony coral taxa, surveys of 100 locations around the island by Zlatarski and Estalella (1982) yielded 55 species (depending on type of classification), of which 13 were ahermatypes, as well as five hydrocorals. Nine hermatypic species reported by these authors were not found in the Guantánamo Bay area: *Acropora prolifera* (only one record for Cuba), *Madracis decactis*, *M. senaria* (only one record), *Solenastrea bournoni*, *S. hyades*, *Cladocora arbuscula*, *Scolymia wellsi*, *Mycetophyllia reesi*, and *Meandrina meandrites braziliensis*. Eight ahermatypic species reported by Zlatarski and Estalella (1982) were not found either, as well as two (*Millepora delicatula* and *M. squarrosa*) of the five hydrocorals. Not unexpectedly, the coral fauna of the south-

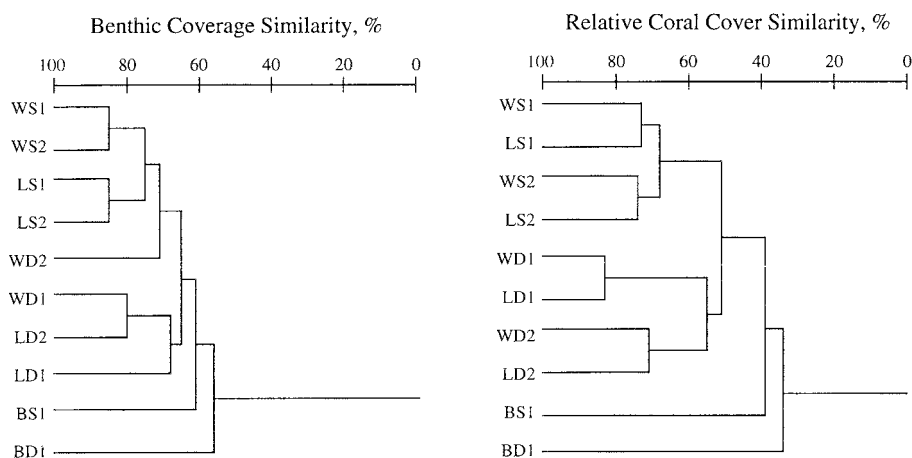


Figure 5. Similarity of reefs based on benthic coverage of all taxa (left) and relative coral coverage (right) at Guantánamo Bay Naval Station, Cuba. Similarity values were computed using the Percent Similarity Index and clustered using a group-average sorting strategy.

eastern Cuban coast is highly similar to other shallow-water (<30 m) Caribbean reef areas (Cairns, 1982; Fenner, 1993; Holst and Guzman, 1993; Chiappone et al., 1996).

Reef zonation has been defined as distinct coral associations dominated by one to a few reef-building species (Goreau, 1959; Geister, 1977). Zones tend to be roughly parallel and correspond to differences in the character of the substrate, light intensity, and degree of wave exposure (Graus and Macintyre, 1989). The assessment of reefs at Guantánamo Bay Naval Station revealed depth-related patterns in coral cover and species composition. Changes in community structure with depth tend to reflect changes in species composition and relative abundance, rather than differences in diversity and absolute abundance (Bak, 1977; Liddell and Ohlhorst, 1987; Fenner, 1993). The pattern of greater coral cover, diversity and evenness measures with depth in the Guantánamo Bay area may reflect greater disturbance in shallow reefs, principally due to wave energy. One of the most notable changes with depth was a shift in dominant coral species: *A. tenuifolia* and *A. palmata*, more abundant at 5-m depth, were replaced at 10-m depth by *A. cervicornis* and *P. porites*.

Algae and stony corals dominated shallow spur-and-groove reefs of Guantánamo Bay. Coral cover among five reefs was equal to or greater than that reported for other western Atlantic reefs (Fenner, 1993; Edmunds and Bruno, 1996; Chiappone and Sullivan, 1997; Chiappone et al., 1997). Dominant species were *A. tenuifolia*, *M. annularis*, *P. porites*. *M. complanata*, and *A. palmata* were locally abundant on individual spurs. This dominance pattern is very similar to western Caribbean reefs such as in Belize, Honduras, and the Cayman Islands (Rutzler and Macintyre, 1982; Fenner, 1993). A characteristic feature of some western Caribbean reefs is the prevalence of *A. tenuifolia* in shallow zones (<7 m) (Fenner, 1993; Aronson and Precht, 1995). On four of the five shallow reefs surveyed at Guantánamo Bay Naval Station, this species covered on average 4 to 5% of the reef surface sampled. This contrasts with reefs in the Greater Antilles, Bahamas, and Florida Keys, where this species is rare or absent (Chiappone and Sullivan, 1997; Chiappone et

al., 1997). *A. tenuifolia* tends to predominate in low-energy conditions, due to its delicate, blade-like colonies (Cairns, 1982; Chornesky, 1991).

An often-characteristic feature of deeper spur-and-groove reefs (10–25 m) in the western Caribbean is the prevalence of *A. cervicornis* (Goreau, 1959; Adey, 1977). Although disease and hurricanes have decimated *A. cervicornis* populations in many locations (Gladfelter, 1982; Knowlton et al., 1990), this species was historically a major mid-depth reef terrace builder throughout the wider Caribbean. In the five deeper spur-and-groove reefs surveyed at Guantánamo Bay Naval Station, the substratum was mostly comprised of live *A. cervicornis* (mean coverage ranging from 0.1 to 9.4%), rubble colonized by algae, or massive coral species. While many of the areas with live *A. cervicornis* were surrounded by rubble, possibly indicative of disease, no incidence of disease was recognizable for any coral species we surveyed.

Among the important factors determining coral abundance, growth, and distribution is sedimentation (Rogers, 1990). At the population level, sedimentation can affect diversity, species composition, and coverage, while growth, recruitment, disease incidence, and recovery potential can be affected at the colony level (Loya, 1976; Cortes and Risk, 1984). Within certain limits, reef-building corals can rid themselves of sediment by such processes as mucus secretion and ciliary action. A second objective of the rapid assessment of Guantánamo Bay coral reefs was to evaluate the differences, if any, in reef community structure among leeward and windward reefs, representing possible differences in sedimentation from the Guantánamo River. Because circulation is predominately from east to west in the study area, we expected leeward reefs to differ in coral cover and relative abundance patterns. It was apparent during SCUBA dives that turbidity during the ebb tide increased dramatically on leeward reefs (15+ m horizontal during flood tide, but less than 3–4 m during ebb tide) and anecdotal observations from Naval Station personnel suggested that development north of the Bay has caused increased sedimentation (P. Martinez, pers. comm., Public Works Department).

Despite qualitative differences in visibility apparent to the underwater observer, quantitative biological data collected during the reef assessment indicated no statistical differences attributable to location in terms of topographic complexity, coral cover, or coral diversity. We anticipated that coral cover and diversity would be lower on leeward reefs, yet the results illustrated instead depth-related patterns consistent for both windward and leeward coasts. There were some differences in relative abundance patterns that potentially indicate a chronic, low-level sedimentation or turbidity effect. For example, *P. porites* was more abundant than *A. cervicornis* on spurs near the mouth of Guantánamo Bay, potentially reflecting the ability of *P. porites* to remove silt-sized particles more efficiently (Hubbard and Pocock, 1972). Other species relatively efficient at sediment removal were more abundant on leeward reefs than windward reefs, such as *D. clivosa* and *S. siderea*. The overland runoff in the study area may partially explain the lack of any statistical effect recorded during our study, as well as the lack of historical data on land-use patterns and resultant effects on nearshore benthos. In contrast, sedimentation impacts have been documented in many other coastal areas of Cuba, particularly near urbanized and industrial areas, but also in many impacted watersheds (Alcolado et al., 1997).

Surveyed reefs at Guantánamo Bay Naval Station indicated dominance by algae, especially algal turfs, and reef-building corals. Relative to other Caribbean reef areas, these results are surprising and appear to differ from the large-scale declines in coral cover and concurrent increases in macroalgae documented in the Lesser Antilles (Smith et al., 1997),

south-central Caribbean (Woodley et al., 1997), and Central America (Cortes, 1997). The very high coral cover values recorded are comparable to results from the central Bahamas (i.e., most sites with >25% cover), although the dominance patterns are remarkably different (Chiappone et al., 1997). Nine of the ten sites surveyed had mean coral cover between 26 and 49%. *A. cervicornis* was locally abundant and comprised nearly 10% of the reef surface in some locations at 10-m depth, contrasting with large-scale declines documented Caribbean-wide from disease, algal overgrowth due to herbivore loss (particularly by urchins because of overfishing), and storm damage (Woodley et al., 1997). *A. palmata* was relatively sparse in distribution, recorded within quadrats at only two locations, and does not appear to form extensive reef crests at Guantánamo Bay. Although the reef flat/breaker zone appears to have been constructed by this species, algae now dominate this zone, and the timing and cause of the *A. palmata* decline are unknown.

Although algae were the predominant benthos in all surveyed reefs, turfs represented most coverage, and all reefs had less than 25% coverage by macroalgae (principally *Halimeda*, *Lobophora*, *Dictyota*). Although the predominance of algal turfs may be indicative of high grazing pressure, no urchins were found in the surveyed quadrats, and *Diadema antillarum* has apparently not recovered elsewhere on Cuban reefs (Alcolado et al., 1997). More surprisingly, the coral reefs at Guantánamo Bay are intensively fished (recreational hook-and-line and spearfishing), with piscivores and large herbivores scarce or totally absent in shallow water (Sedaghatkish and Roca, 1999).

Tropical storms represent significant perturbations which can affect coral reefs through physical destruction, through increases in sedimentation and turbidity, and through lowering of salinity and increasing of nutrient concentrations after heavy runoff (Rogers et al., 1982). Physical destruction can result in changes in diversity (e.g., reduction in species, changes in relative abundance), competitive interactions, and reductions in topographic complexity and coral cover (Knowlton et al., 1990; Rogers et al., 1991). A wide range of damage to reefs may occur, dependent upon the intensity of the storm, proximity of the storm eye to the reef, reef exposure, and a variety of other factors (Rogers et al., 1991). From 1944 through 1996, 14 tropical storms of varying severity have come within 200 km of Guantánamo Bay. The most recent storm was Hurricane Gordon in 1994, however, this was only a tropical storm (wind speed = 74 km h⁻¹) near the study area. Of the 14 tropical storms, only seven have been of hurricane strength (>110 km h⁻¹), and all but one of the hurricanes occurred before 1967. Because there are no historical data for reefs in southeastern Cuba, determining the impacts of past storms are speculative at best. It is evident, however, that several reef systems in the western Caribbean which have not been impacted by storms in the past two decades (e.g., Roatan, Cayman Islands) have greater coral cover and structural complexity (Rogers et al., 1991; Fenner, 1993). Perhaps the rarity of destructive storm events at Guantánamo Bay, compared to other areas such as northern Jamaica, has allowed corals to continue to flourish, despite apparent outbreaks of disease and low herbivore densities (urchin mortality and overfishing).

ACKNOWLEDGMENTS

The U.S. Department of Defense, Department of the Navy, University of Miami, and The Nature Conservancy's Caribbean Division provided financial and logistical support. The authors would like to thank T. Loop, P. Martinez, and J. MacDougal of the Naval Station's Office of Environmental Regulation, Public Works Division, CPO G. Horton, R. Gomez of University of Miami-RSMAS

for dive support, R. Roach of Evans Environmental and R. Wright of The Nature Conservancy. R. B. Aronson, J. Garzon-Ferreira and J. W. Tunnell provided helpful comments to an earlier version of the manuscript.

LITERATURE CITED

- Adey, W. H. 1977. Shallow water Holocene bioherms of the Caribbean Sea and West Indies. Proc. 3rd Int'l. Coral Reef Symp., Miami. 2: xxi-xxiii.
- Alcolado, P. M., R. Claro, G. Menendez, P. Garcia-Parrado and B. Martinez-Daransas. 1997. Status of Cuban coral reefs. Proc. 8th Int'l. Coral Reef Symp., Panama City 1: 341-344.
- _____, A. Herrera-Moreno and N. Martinez-Estalella. 1993. Sessile communities as environmental bio-monitors in Cuban coral reefs. Pages M1-M7 in R. N. Ginsburg, compiler. Global aspects of coral reefs: Health, hazards, and history, Univ. Miami, Rosenstiel School of Marine and Atmospheric Science, Florida.
- Aronson, R. B. and W. F. Precht. 1995. Landscape patterns of reef coral diversity: A test of the intermediate disturbance hypothesis. J. Exp. Mar. Biol. Ecol. 192: 1-14.
- Bak, R. P. M. 1977. Coral reefs and their zonation in Netherlands Antilles. Pages 3-16 in S. H. Frost, M. P. Weiss and J. B. Saunders, eds. Reefs and related carbonates-ecology and sedimentology, Studies in Geology, no. 4 Am. Assoc. Petroleum Geologists, Tulsa, Oklahoma.
- Bros, W. E. and B. C. Cowell. 1987. A technique for optimizing sample size (replication). J. Exp. Mar. Biol. Ecol. 114: 63-71.
- Cairns, S. D. 1982. Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize. Pages 271-302 in K. Rutzler and I. G. Macintyre, eds. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities, Smithsonian. Inst. Press, Washington, D.C.
- Chiappone, M. and K. M. Sullivan. 1997. Rapid assessment of reefs in the Florida Keys: Results from a synoptic survey. Proc. 8th Int'l. Coral Reef Symp., Panama City. 2: 1509-1514.
- _____, _____ and C. Lott. 1996. Hermatypic scleractinian corals of the south-eastern Bahamas: A comparison to western Atlantic reef systems. Carib. J. Sci. 32: 1-13.
- _____, _____ and R. Sluka. 1997. Status of reefs in the central Bahamas based on a large-scale survey. Proc. 8th Int'l. Coral Reef Symp., Panama City. 1: 345-350.
- Chornesky, E. A. 1991. The ties that bind: inter-clonal cooperation may help a fragile coral dominate shallow high-energy reefs. Mar. Biol. 109: 41-51.
- Cortes, J. 1997. Status of the Caribbean coral reefs of Central America. Proc. 8th Int'l. Coral Reef Symp., Panama City. 1: 335-340.
- _____, _____ and M. J. Risk. 1984. El arrecife coralino del Parque Nacional Cahuita, Costa Rica. Rev. Biol. Trop. 32: 109-121.
- Edmunds, P. J. and J. F. Bruno. 1996. The importance of sampling scale in ecology: kilometer-wide variation in coral reef communities. Mar. Ecol. Prog. Ser. 143: 165-171.
- _____, D. A. Roberts and R. Singer. 1990. Reefs of the northeastern Caribbean. I. Scleractinian populations. Bull. Mar. Sci. 46: 780-789.
- Fenner, D. P. 1993. Some reefs and corals of Roatan (Honduras), Cayman Brac, and Little Cayman. Atoll Res. Bull. 388: 1-30.
- Field, J. G., K. R. Clarke and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8: 37-52.
- Geister, J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. Proc. 3rd Int'l. Coral Reef Symp., Miami. 1: 23-29.
- Gladfelter, W. B. 1982. White-band disease in *Acropora palmata*: Implications for the structure and growth of shallow reefs. Bull. Mar. Sci. 32: 639-643.
- Gleason, H. A. 1922. On the relation between species and area. Ecology 3: 158-162.
- Goreau, T. F. 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. Ecology 40: 67-90.

- Grant, C. J. and J. R. Wyatt. 1980. Surface currents in the Eastern Cayman and Western Caribbean Seas. *Bull. Mar. Sci.* 30: 613–622.
- Graus, R. R. and I. G. Macintyre. 1989. The zonation patterns of Caribbean coral reefs as controlled by wave energy and light energy input, bathymetric setting and reef morphology: computer simulation experiments. *Coral Reefs* 8: 9–18.
- Herrera, A. and P. Alcolado. 1986. Estructura ecológica de las comunidades de gorgonáceos del arrecife de Santa Cruz del Norte. Reporte de Investigación del Instituto de Oceanología, Academia de Ciencias de Cuba No. 49. 27 p.
- Holst, I. and H. M. Guzmán. 1993. Lista de corales hermatípicos (Anthozoa: Scleractinia; Hydrozoa: Milleporina) a ambos lados del istmo de Panamá. *Rev. Biol. Trop.* 41: 871–875.
- Hubbard, J. A. E. B. and Y. P. Pocock. 1972. Sediment rejection by recent scleractinian corals: a key to paleo-environmental reconstruction. *Geolog. Rund.* 61: 598–626.
- Knowlton, N., J. C. Lang and B. D. Keller. 1990. Case study of natural population collapse: Post-hurricane predation on Jamaican staghorn corals. *Smithson. Contrib. Mar. Sci.* 31. 25 p.
- Kuhlmann, D. H. H. 1974. The coral reefs of Cuba. *Proc. 2nd Int'l. Coral Reef Symp., Brisbane.* 2: 69–83.
- Liddell, W. D. and S. L. Ohlhorst. 1987. Patterns of reef community structure, north Jamaica. *Bull. Mar. Sci.* 40: 311–329.
- Loya, Y. 1976. Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull. Mar. Sci.* 26: 450–466.
- Milliman, J. D. 1973. Caribbean coral reefs. Pages 1–50 in O. A. Jones and R. Endean, eds. *Biology and geology of coral reefs*, vol. 2. Biology 1. Academic Press, New York.
- Ohlhorst, S. L., W. D. Liddell, R. J. Taylor and J. M. Taylor. 1988. Evaluation of reef census techniques. *Proc. 6th Int'l. Coral Reef Symp., Townsville.* 2: 319–324.
- Pielou, E. C. 1977. *Mathematical ecology*. Wiley & Sons, New York. 385 p.
- _____. 1984. *The interpretation of ecological data. A primer on classification and ordination*. Wiley & Sons, New York. 263 p.
- Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser.* 62: 185–202.
- _____, M. Gilnack and H. C. Fitz. 1983. Monitoring of coral reefs with linear transects: A study of storm damage. *J. Exp. Mar. Biol. Ecol.* 66: 285–300.
- _____, L. N. McLain and C. R. Tobias. 1991. Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. *Mar. Ecol. Prog. Ser.* 78: 189–199.
- _____, T. H. Suchanek and F. A. Pecora. 1982. Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bull. Mar. Sci.* 32: 532–548.
- Rutzler, K. and I. G. Macintyre. 1982. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. Pages 9–45 in K. Rutzler and I. G. Macintyre, eds. *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities*. Smithsonian. Inst. Press, Washington, D.C.
- Sedaghatkish, G. and E. Roca, eds. 1999. *Rapid ecological assessment: U.S. Naval Station Guantánamo Bay, Cuba*. The Nature Conservancy, Arlington, Virginia. 268 p.
- Smith, A. H., C. S. Rogers and C. Bouchon. 1997. Status of western Atlantic coral reefs in the Lesser Antilles. *Proc. 8th Int'l. Coral Reef Symp., Panama City.* 1: 351–356.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*, 2nd ed. W. H. Freeman and Company, New York. 859 p.
- Underwood, A. J. 1981. Techniques for analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.* 19: 513–605.
- Wells, S. M. 1988. Coral Reefs of the World, vol. 1. Pages 131–136 In *Atlantic and Eastern Pacific*. IUCN Conservation Monitoring Centre, Cambridge, UK.
- Woodley, J. D., K. De Meyer, P. Bush, G. Ebanks-Petrie, J. Garzon-Ferreira, E. Klein, L. P. J. J. Pors and C. M. Wilson. 1997. Status of coral reefs in the south central Caribbean. *Proc. 8th Int'l. Coral Reef Symp., Panama City.* 1: 357–362.

- Zar, J. H., 1996. Biostatistical analyses, 3rd rd. Prentice Hall, New Jersey. 918 p.
- Zlatarski, V. N. and N. M. Estalella. 1982. Les Scléractiniaires de Cuba. Editions de l'Académie Bulgare des Sciences, Sofia, Bulgaria. 453 p.

ADDRESS: (M.C.) *National Undersea Research Center, University of North Carolina at Wilmington, 515 Caribbean Drive, Key Largo, Florida 33037*; (K.S.S.) *Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, Florida 33124*; (G.B., J.T.) *The Nature Conservancy, Caribbean Division, 4245 N. Fairfax Drive, Suite 100, Arlington, Virginia 22203*.

Appendix. Continued.

Bottom type	WS1	WD1	WS2	WD2	LS1	LD1	LS2	LD2	BS1	BD1
<i>Leptoseris cucullata</i>					0.1					
<i>Madracis formosa</i>					0.1					
<i>M. mirabilis</i>	0.2	0.5		0.6				0.1		0.5
<i>Meandrina meandrites</i>			0.4		0.6				0.1	
<i>Millepora alcicornis</i>		0.1	0.2		0.2					
<i>M. complanata</i>	2.7	0.3	1.5	0.1	2.5	1.6	1.8	0.4	0.3	0.3
<i>Montastraea annularis</i>	11.0	24.5	7.4	7.0	5.4	22.1	3.6	11.7	0.8	3.3
<i>M. cavernosa</i>		0.7	0.6	0.2		1.0	0.4	0.2	0.3	0.1
<i>Mussa angulosa</i>	0.1									
<i>Mycetophyllia danaana</i>			0.1	0.2	0.1	0.2				
<i>M. ferox</i>						0.2		0.1		
<i>Porites astreoides</i>	3.5	1.8	4.9	0.9	3.8	2.3	4.4	2.9	2.5	1.3
<i>P. porites</i>	2.4	3.2	6.7	13.0	1.3	4.8	3.1	16.4	0.9	39.8
<i>Siderastrea siderea</i>	0.9	2.3	1.6		3.6	2.4	2.6	0.4	4.0	0.2
<i>Steph. michelini</i>		0.2			0.1		0.3	0.5		
Total coral cover	30.1	37.9	29.3	34.4	29.8	40.2	26.1	37.2	10.7	49.2
<i>Briareum asbestinum</i>	0.3		0.3		0.6		0.2			
<i>Erythro. caribaeorum</i>	0.7		0.5	0.1	0.9	0.2	0.7	0.1		
<i>Eunicea mammosa</i>	0.2	0.2	0.2	0.1	0.1	0.1				
<i>E. palmeri</i>				0.2						
<i>E. tourneforti</i>			0.2			0.1	0.1		0.1	
<i>Gorgonia flabellum</i>						0.1				
<i>G. ventalina</i>		0.2	0.1	0.1	0.2	0.1	0.1		0.3	
<i>Muricea muricata</i>		0.1		0.1		0.1				
<i>Muriceopsis flavida</i>					0.2					
<i>Plexaura flexuosa</i>	0.1	0.3		0.1		0.5	0.3			
<i>P. homomalla</i>		0.2	0.3	0.1	0.3		0.2	0.1		
<i>Plexaurella dichotoma</i>	0.1	0.1		0.1			0.1			
<i>P. nutans</i>								0.1		0.1
<i>Pseudoplex. porosa</i>	0.1		0.1		0.1					
<i>Pseudopter. acerosa</i>								0.1		
<i>P. americana</i>			0.2		0.1				0.2	
Total octocoral cover	1.0	1.1	2.1	0.9	2.0	1.3	1.8	0.9	0.7	0.1
<i>Lebrunia danae</i>							0.1			
<i>Palythoa mammosa</i>	1.0		1.6		0.5	0.4	0.8	0.2		